THE CLASSIFICATION OF COLEOPTERA*

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Leng in his Catalogue of the Coleoptera of America north of Mexico, 1920, and in its second supplement, 1933, summarized the attempts that had been made up until then to bring the classification of beetles into line with probable phylogeny. The important results of Bøving and Craighead on larvae remained wholly uncorrelated with the evidence obtainable from adult structures, until an important paper by Peyerimhoff appeared in 1933. (Les larves des Coleoptères d'aprés A. Bøving et F. C. Craighead et les grandes critériums de l'ordre). Lameere in 1938 (Precis de Zoologie) published his final revised views on the classification of the order, emphasizing the work of Max Poll, one of his own students, and others on cryptonephridism, but on the whole an improvement. To all that has been done before Drs. Jeannel and Paulian (Morphologie abdominale des Coléoptères et systématique de l'ordre, 1944) have now added their work on the reduction of the sternites, and on the types of male genitalia.

A study of the last mentioned paper suggests that there may have been certain phylogenetic relationships that are not clearly brought out in it. To illustrate these graphically I have prepared the accompanying phylogenetic tree.

Coleoptera have descended from Megaloptera. The correspondences between their larvae, as Lameere remarks, are too numerous and too close to permit of any other interpretation. The base of the tree (1) represents, therefore, the common prototype of the two. The larva of this protype was aquatic, thysanuriform, active, and predaceous. Instead of prolegs the leg-rudiments of the abdominal segments 1 to 9 have been re-utilized to form gills, the tenth segment terminated in two pairs of hooks. The tibia and tarsus were separate, the latter terminating in a pair of claws. The adult had many segmented, filiform antennae, five segmented tarsi, six free malpighian tubes, tubular testes, polytrophic ovarioles, and genitalia of the three-lobed tpye.

This prototype differed from that of all other Holometabola in that the pupal covering was secreted by the malpighian tubes, instead of being spun from labial silk, and likewise by the absence of prolegs. The changes that it underwent in becoming a beetle were few: the larvae acquired pseudocerci (urogomphi); the adults, in developing elytra acquired a more perfect protection for their functional but now folded wings than had been previously known and in so doing were fitted for the initiation of the conquest of the infinite diversity of confined environments that has made the order successful and prodigious above all other living creatures. In addition the number of antennal segments was set at eleven, the first sternite, cerci, and male gonopods lost, the male developed accessory glands on the ejaculatory duct that produce a spermatophore, and the ninth abdominal segment became invaginated.

From this ancestral coleopteron there have arisen two lines of descent, the Adephaga, and the Polyphaga. The Adephaga constitute a

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group, say Jeannel and Paulian, so separate by all its characters, morphological, anatomical, and larval that one is tempted to make it an order apart. And yet they are the original Coleoptera. There is nothing of any importance by way of change from the prototype that we can say about either larva or adult. In fact the larva of Gyrinoidea differ in no essential respect from those of Megaloptera, except that an extra pair of gills on segment 9 are probable precursors of pseudocerci, and one is tempted to wonder whether they are not migrants. The numerous adaptations of the adult to life on the surface of the water are strictly neogenetic, less advanced in Oligocene fossils, and of no significance in placing the origin of the group. I have no doubt that the aquatic larvae of Adephaga have had a continuously aquatic history that traces back to Protoperlaria and even to the earliest ptilote insects. But within the Adephaga there have been two lines of specialization, the one has been a tendency on the part of the adults to follow the lead of their larvae and become in their turn aquatic, the other has been for the larvae to become terrestrial, and in such case the adults never became aquatic. This is the case with Carabidae, Rhysodidae, and Cupedidae.

There is no occasion to constitute a third suborder for Cupedidae. Their fundamental characters are those of the Adephaga, and hence of the archetypal coleopteron. Persons have been misled in interpreting the adaptive characters that have fitted them for a xylophilous life, and that have been paralleled polygenetically many times in the Polyphaga, as indicating a relationship with the latter. There is none, merely similarity. However we know nothing of their internal anatomy, and when this lacuna is supplied it may appear that their proper origin is between 2' and 3' on the tree.

The more important changes at 3' that have produced the Polyphaga are: the tibia and tarsus of the larva have fused and the claw become single; in the adult the propleural plates have become concealed by the pronotal flanks, the testes are of the type that Lameere terms 1b, that is the follicles are sessile, verticillate, and arranged around the vas deferens, and the ovarioles have become teletrophic.

The full complement of seven sternites was present in the archetype of Polyphaga from which the Cantharoidea depart in no important respect except that the larvae have for the most part become terrestrial, and have lost the segmentation of their pseudocerci. But some are aquatic and possess tracheal gills. It would seem that Lameere as well as Jeannel and Paulian were wise in beginning the Phytophaga with these beetles.

At 6' there has been a change in the testes to what Lameere terms type 1a, with the follicles sessile, but fasciculate, arranged at the end of the vas deferens. It is possible that this is the primitive type, and that the Cantharoidea have developed type 1b as a specialization.

At 7, the stem of Staphylinoidea + Scarabaeoidea, in the adult sternite 2 has become invaginated, absent medially but distant and visible at the sides. The antennae have become clavate. The larva of the primitives are still aquatic, doubtless continuously so, and the lateral processes on the abdominal segments of Spercheus suggest the retention of modified gills.

The Scarabaeoidea are a very clear-cut group in which the antennal club of the adult in becoming asymmetric has become lamelliform;

the testes are of a special type not occurring elsewhere (but approached in Phytophaga) the accessory glands of the ejaculatory duct have been lost, and the male genitalia have undergone characteristic modifications not paralleled elsewhere.

Returning to the main (cantharid-like) stem, two important changes have occurred that set apart all of the lines that follow: The distal ends of the malpighian tubes have become concealed under the membrane that surrounds the proctodaeum, a condition known as cryptonephredism. In the larvae the pseudocerci have become single-segmented immobile horns or hooks, but in more specialized offshoots may disappear entirely.

Branch 9, Tenebrionoidea, is characterized by a particular type of male genitalia, invaginated, the phallobase forming a dorsal sheatth, and after the differentiation of the Meloidae, the second sternite has become completely lost. This last has also occurred at 9', evidently independently, since it is not accompanied by the type of genitalia characteristic of all of the male Tenebrionoidea, including Meloidae.

9', at which point sternite 2 has disappeared, represents a platform for the ultimate evolution of the order, more and more difficult to decipher. The branches Dascylloidea, Cleroidea, and Cucujoidea, I accept more on the conviction of Drs. Jeannel and Paulian than my own. In the former two the male genitalia have each developed a characteristic type, but in the primitives of the Cucujoidea they have retained the primitive three-lobed coleopterous type. The best we can say here is that evolution has become "explosive" with many different lines resulting, which are difficult to assemble in main trunks, the latter being at best opinionative.

The final branch, 11''', on the contrary is a very distinct one, culminating in high specialization. All of them phytophagous, reaching in this respect their highest culmination in the ambrosia beetles, the adults have in common the well-known cryptopentamerous tarsi, bristly beneath, and testes of type two as in the Scarabaeoidea, but differing in each consisting of only 1 or 2 pedunculated testiculi. As in that group, which are likewise principally vegetarian, the ejaculatory duct is without accessory glands, and no spermatophore is formed. The male genitalia are of a uniform type that we may call saddled - Jeannel and Paulian say "tegmen en cavalier." The larvae are stout, eruciform, with short legs (or none) and have lost their pseudocerci. Jeannel and Paulian note that this group is perfectly homogeneous, that all characters of the adult point to a narrow parentage among the several families, and that they must be retained as a unit.

From the foregoing it becomes apparent that the division of Polyphaga into two further suborders was not a happy suggestion on the part of Jeannel and Paulian, partly because the Cantharoidea stand at the base of each. The wiser course seems to be to restrict the rank of suborder to basic divisions like Adephaga and Polyphaga that differ in many fundamental characters. One could make a division, lesser in rank than suborder, between 6' and 7', cutting off the Tenebrionoidea - Dascylloidea - Cleroidea - Cucujoidea - Cerambycoidea as Cryptonephridia, but in that case the Cantharoidea would seem better placed with the Staphylinoidea and Scarabaeoidea in a contrasting more primitive group to which Lameere has applied the term "Haplonephridia." This is fundamentally the classification of Lameere, except that he has included some families of Dascylloidea in his Haplonephridia, on the grounds of their having free malpighian tubes. According

to Jeannel and Paulian this is not the case, even in Elateridae, which are on this account not separated widely from the Buprestidae, as Lameere had thought necessary.

It will be noted that Jeannel, as a result of his extensive work with ground beetles has greatly augmented the number of families of Caraboidea, and suggests that detailed study will necessitate the same procedure in other superfamilies. That is one method of taxonomic procedure. To the author it seems ill-advised for it results in a complex classification, too ponderous to be readily comprehended, and with no compensatory advantage. In fact one seems by this process to lose sight of the very aim of classification. It seems better to call the 39 families of Jeannel's Caraboidea all subfamilies of Carabidae.

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CLASSIFICATION OF COLEOPTERA

By Jeannel and Paulian, 1946

I. SUBORDER HETEROGASTRA

1. Division MALACODERMOIDEA

   a. Section Lymexylaria. Lymexylidae, Micromalthidae.
   b. Section Lampyridaria. Drilidae, Lycidae, Karumiidae, Lampyridae, Cantharidiidae.

2. Division HETEROMEROIDEA

   a. Section Lyttaria. Meloidae, Trictenotomidae.
   b. Section Tenebrionaria. Tenebrionidae. Alleculidae, Lagriidae, Melandryidae. Othniidae, Pedilidae, Aegialitidae, Pythidae, Pyrochroidae. Discolomidae, Filionidae, Rhysopaussidae, Anthicidae.
   c. Section Mordellaria. Mordellidae, Anaspidae, Rhipiphoridae.
   d. Section Oedemeraria. Oedemeridae, Scraptiidae.

3. Division CLEROIDEA

   a. Section Cleraria. Cleridae.
   b. Section Melyridaria. Melyridae.

4. Division DASCILLOIDEA

   a. Section Dascillaria. Dascillidae, Helodidae, Psephenidae, Eucinetidae, Ptilodactylidae?, Eurypogonidae?
   b. Section Sternoxia. Rhipiceridae, Cebrionidae. Cerophytidae, Phylloceridae, Elateridae, Throscidae, Eucnemididae, Buprestidae.
   c. Section Anobiaria. Anobiidae, Ptinidae, Ectrephidae.

5. Division CUCUJOIDEA

   a. Section Dermestaria. Dermestidae, Lyctidae.
   b. Section Byrrharia. Dryopidae, Georyssidae, Byrrhidae, Nosodendridae.
   c. Section Thorictaria. Thorictidae.
   d. Section Mycetophagaria. Mycetophagidae, Derodontidae, Monoedidae.
   e. Section Colydiaria. Byturidae, Boridae, Monommaridae, Colydiidae, Cisidae. Ostomatidae, Psoidae, Cyathoceridae.
   f. Section Bostrycharia. Bostrychidae.
   g. Section Cucujaria. Nitidulidae, Phalacridae, Monotomidae. Corylophidae. Rhizophagidae, Cucujidae, Erotylidae, Cryptophagidae, Sphindidae, Lathridiidae. Heteroceridae.
   h. Section Aglycyderaria. Aglycyderidae, Proterrhinidae.
   i. Section Coccinellaria. Coccinellidae, Enfomychidae.

6. Division PHYTOPHAGOIDEA. Cerambycidae, Chrysomelidae, Bruchidae, Anthribidae. Brenthidae, Curculionidae, Scolytidae, Platypodidae.

II. SUBORDER HAPLOGASTRA

1. Division STAPHYLINOIDEA.

   a. Section Catopiaria. Catopidae, Liodidae, Leptinidae, Camiaridae, Clambidae, Colonidae. Ptiliidae, Hydroscaphidae, Sphaeriidae, Hydraenidae.
   b. Section Brachelytra. Silphidae, Staphylinidae, Scaphidiidae, Pselaphidae, Scymaenidae.
   c. Section Histeraria. Histeridae, Synteliidae, Sphaeritidae.
   d. Section Palpicornia. Hydrophilidae, Spercheidae, Helophoridae, Sphaeridiidae.

2. Division SCARABAEOIDEA. Lucanidae, Passalidae, Trogidae, Acanthoceridae. Geotrupidae, Hybosoridae, Scarabaeidae.

III SUBORDER ARCHOSTEMATA

Cupedidae.

IV. SUBORDER ADEPHAGA

1. Division CARABOIDEA.

   a. Section Isochaeta. Trachypachidae, Gehringiidae, Metriidae, Ozaenidae, Paussidae.
   b. Section Simplicia. Carabidae, Nebriidae, Elaphridae, Migadopidae, Omophronidae, Loroceridae, Cicindelidae, Siagonidae, Cymbionotidae.
   c. Section Scrobifera. Hiletidae, Scaritidae.
   d. Section Stylifera. Apotomidae, Broscidae, Psydridae, Trechidae, Patrobidae.
   e. Section Conchifera. Perigonidae, Cnemacanthidae, Peleciidae, Melanodidae, Harpalidae, Pterostichidae. Callistidae, Glyptidae, Panagaeidae, Licinidae. Odacanthidae, Masoreidae, Lebiidae, Anthiidae, Zuphiidae, Dryptidae.
   f. Section Baltifera. Brachinidae, Pseudomorphidae.

2. Division HALIPLOIDEA. Haliplidae.

3. Division HYGROBIOIDEA. Hygrobiidae, Amphizoidae.

4. Division RHYSODOIDEA. Rhysodidae.

5. Division DYTISCOIDEA. Dytiscidae, Noteridae.

6. Division GYRINOIDEA. Gyrinidae.

A SUGGESTED REARRANGEMENT OF THE MAJOR CATEGORIES OF JEANNEL AND PAULIAN'S CLASSIFICATION

I. SUBORDER ADEPHAGA

Superfamily Gyrinoidea
Superfamily Caraboidea (Including Halipoidea, Hygrobioidea, Rhysodoidea, and Dytiscoidea)
Superfamily Cupedoidea (Archostemmata)

II. SUBORDER POLYPHAGA

1. Superfamily Cantharoidea (Malacodermoidea)
2. Superfamily Staphylinoidea
3. Superfamily Scarabaeoidea

4. Superfamily Tenebrionoidea (Heteromeroidea)
5. Superfamily Dascilloidea
6. Superfamily Cleroidea
7. Superfamily Cucujoidea
8. Superfamily Cerambycoidea (Phytophagoidea)

CHARACTERS OF THE PROTOTYPE, AND SUCCESSIVE CHANGES SUPPOSED TO HAVE OCCURRED AT EACH CORRESPONDING POINT IN THE PHYLOGENETIC TREE

1. Prototype for Holometabola (Neuropteroid division)

Adult. Antennae filiform, many-segmented; occipital suture present; pleura not covered by pronotum; wings with primitive venation; tarsi 5-segmented; abdomen with 10 segments; 1st sternite developed; cerci present; ♂ with gonopods, genitalia of 3-lobed type (parameres + aedeagus); accessory glands on the ejaculatory duct produce a spermatophore; ♀ without ovipositor.

Six free malpighian tubes; testes tubular; ovarioles polytrophic (ova accompanied by groups of nurse-cells).

Larva. Thysanuriform, active, predaceous, aquatic; tibiae and tarsus distinct; 2 movable tarsal claws; without prolegs, but with 9 pairs of lateral gills arising from embryonic buds of leg-appendages; 10th sternite tubular, ending in 2 pairs of hooks.

Pupa. Free; covering secreted by malpighian tubes of larva (no labial silk).

2. Male genitalia membranous.

2' Prototype for Coleoptera.

Adult. Antennal segments 11; front wings become elytra; venation of hind wings distorted; of cupedid type, oblongum formed, and cross-veins form cells in cubito-anal region; first sternite lost; sternite 9 invaginated; cerci lost; ♂ gonopods lost.

Larva. Pseudocerci developed on segment 9.

3. Prototype for Adephaga.

Adult. Alula of elytra lost.
Malpighian tubes reduced to 4.

4. Adult. Sternite 2 partly connate with 3, and 3 with 4.
Sternite 10 lost.

5. Adult. Numerous neogenetic adaptions to predaceous life on surface of water. Gyrinoidea.

5' Adult. Sternite 8 invaginated, so that only 6 sternites are visible.

Larva. Lateral pairs of gills lost; terminal hooks of segment 10 lost. Caraboidea.

4' Adult. Sternite 2 invaginated and not visible; sternite 8 invaginated; sternite 10 a pointed strap; internal anatomy not known; aedeagus with supplementary lobes.

Larva. Terrestrial and with neogenetic adaptations to Xylophilous life, paralleling certain Polyphaga; claws single, bifurcate; pseudo-cerci lost. Cupedoidea.

3' Prototype for Polyphaga.

Adult. Occipital suture lost; propleural plates concealed by flanks of pronotum; oblongum replaced by "apertum" and cross-veins reduced; remnant of sternite 10 lost, testes follicular, of type 1 b (i.e., the follicles sessile, verticillate, arranged around the vas deferens); ovarioles teletrophic (nurse-cells remain in apical chamber).

Larva. Tibia and tarsus fused; claws single; lateral gills reduced (or lost?)

6. Adult. Alula of elytra lost.

Larva. Terrestrial. Cantharoidea.

6' Adult. Testes of type 1 a (i.e. the follicles sessile, but fasciculate, arranged at the end of the vas deferens).

7. Adult. Antennae become clavate; sternite 2 invaginated, absent medially but, distinct and visible at the sides. Staphylinoidea.

8' Adult. Segments of club become asymmetric, producing lamellate type; front legs fossorial; testes of type 2, (i.e. each with several stalked testiculi, in which 2 to 12 follicles are arranged radially in a common covering); accessory glands of ejaculatory duct lost; aedeagus largely membranous, the phallobase very enlarged, drum-like.

Larva. Melolonthiform; scatophilous, xylophilus, or feeds on plant tissues, living in confined environment and moving on their side; pseudocerci lost (but not in pupa). Scarabaeoidea.

7' Adult. Distal ends of malpighian tubes concealed under membrane that surrounds the proctodaeum (cryptonephridism).

Larva. Pseudocerci reduced to a pair of single-segmented, immobile horns or hooks.

9. Adult. ♂ genitalia of the invaginated type, the phallobase (tegmen) forming a dorsal sheath. Tenebrionoidea.

10. Larva. Undergo hypermetamorphosis. (Meloidae).

10' Adult. Tarsi heteromerous; sternite 2 has invaginated and disappeared.

Larva. Elongate, very short legs. (Other Tenebrionoidea).

9' Adult. Sternite 2 has evaginated and disappeared.

11. Adult. Aedeagus articulated by several condyles. Dascilloidea.

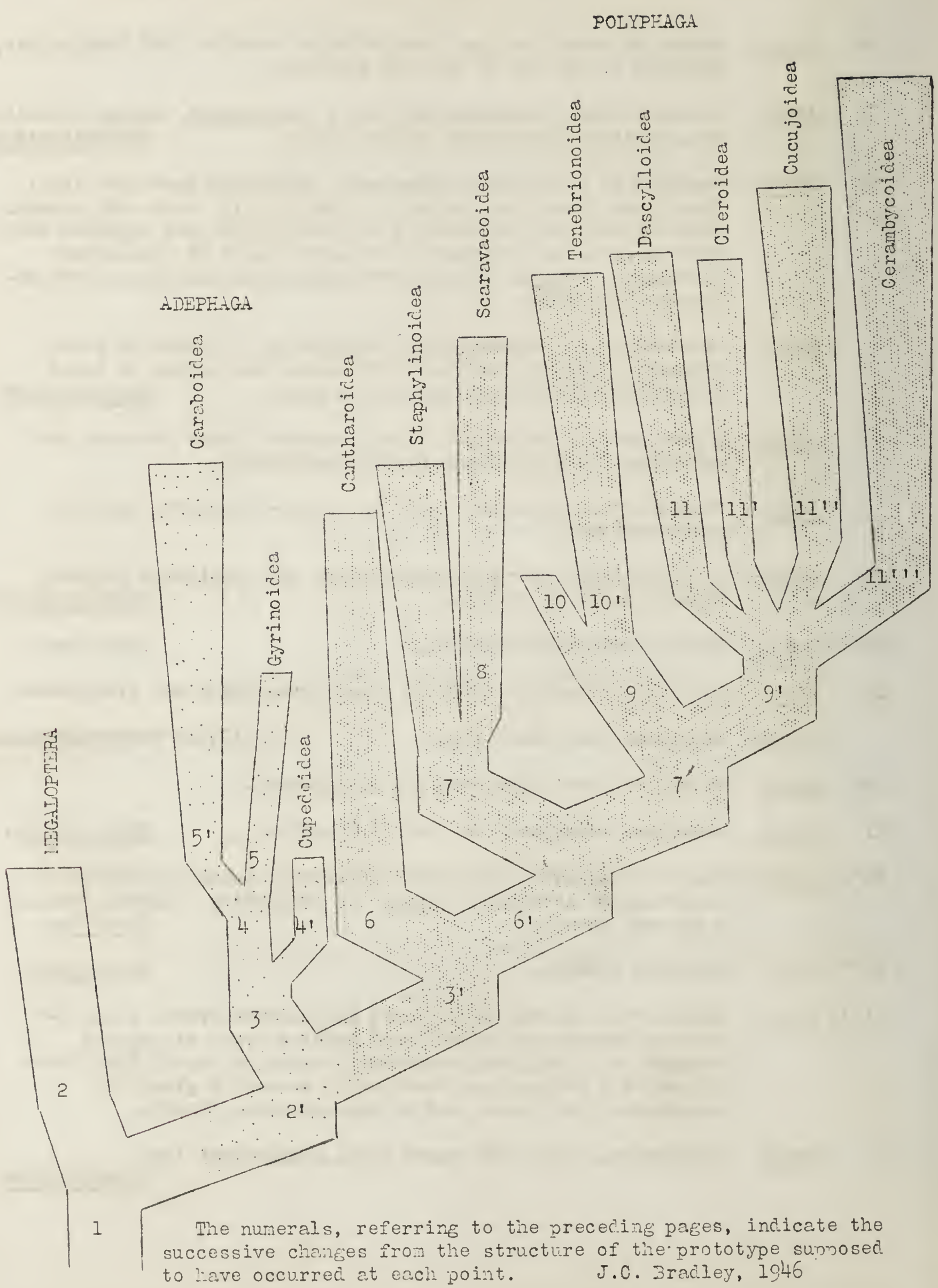
11'. Adult. Flagellar segments asymmetric (serrate), becoming clavate; ♂ genitalia of invaginated type, the phallobase (tegmen) forming a ventral sheath. Cleroidea.

11'' Adult. Antennae clavate. Cucujoidea.

11''' Adult. Median cell of wing open; tarsi cryptopentamerous, segm. 1-3 bristly beneath; ♂ genitalia of saddled type; sternite 9 reduced to a "spiculum gastrale"; testes of type 2 (follicles in one or 2 pedunculate testiculi); accessory glands of ejaculatory duct lost, and no spermatophore formed.

Larva. Vegetarian, stout with short legs; pseudocerci lost. Cerambycoidea.

PHYLOGENETIC TREE OF COLEOPTERA



The numerals, referring to the preceding pages, indicate the successive changes from the structure of the prototype supposed to have occurred at each point. J.C. Bradley, 1946